

THE 1993 PRESIDENTIAL ADDRESS—PART 2 SOME OBSERVATIONS ON THE PROS AND CONS OF BEING A BARK-FEEDING INSECT

DAVID LONSDALE

*Forestry Authority Research Station, Alice Holt Lodge, Wrecclesham, Farnham,
Surrey GU10 4LH.*

The bark of woody plants offers special advantages for insects that use it as a food source. Under its outer corky layer (periderm), it contains relatively succulent tissues (phloem and in some cases cortex) which are a much better source of carbohydrates and amino-acids than the underlying wood. It can therefore be compared nutritionally with leaves and young shoots, but it provides a resource that is not available to insects that feed on the green tissues of deciduous trees; that is, a habitat in which survival and even development can take place throughout the year, given a sufficiently mild winter climate.

Although bark is one of the few year-round food sources available to phytophagous insects in woodlands, it is a strongly defended tissue in many woody plant species. The need for defences against bark-feeding insects becomes clear when we consider how important bark is for a tree's survival. The evolutionary success of trees and shrubs has depended on their ability to form and maintain a long-lived woody cylinder, which in turn depends on the presence of a largely intact covering of bark. The bark overlies the vascular cambium which lays down annual rings of both bark and wood, and its own inner layers include the phloem which is essential for the translocation of sugars and other assimilates. The outer bark (periderm), provides a vital protection for all the perennial parts of the plant, preventing excessive moisture loss and the entry of pathogenic micro-organisms. If an area of bark is killed or removed, it can usually be replaced only through the rather slow process of occlusion, which involves the inward growth of new tissues from around the edge of the damaged area.

As I have mentioned, the protection of the woody cylinder by bark needs to be long-term. Since some tree species can live for several or even many centuries, the need for good defences against attack by bark-feeding insects and micro-organisms is paramount. Defences in bark can be broadly divided into chemical and structural types. Chemical defences make bark tissues unpalatable or toxic, while structural defences take the form mainly of physical barriers. There is some overlap between these two categories, as I shall explain later. As with all forms of defence, including human armaments, there is a price to be paid in the diversion of resources which might otherwise fuel faster growth. In the case of trees, fast growth has advantages for competition for space within the forest canopy. To some extent, trees can minimize their defence expenditure by producing certain kinds of defence only after damage begins to occur. These responsive defences contrast with pre-formed ones, which are an unavoidable cost to the plant. As I shall show, using some specific examples, the dual system of "strategic" and "tactical" defence can involve both chemical and structural mechanisms.

The effectiveness of defence mechanisms in bark is demonstrated by the fact that a largely intact covering of bark is the norm, even on old trees. However, bark is too good a source of nutrients for its defences to have gone unchallenged. Thus, bark-feeding insects have evolved strategies by which the defences of bark can to some extent be overcome or evaded. The resulting interactions between bark-feeding

insects and their hosts are fascinating, and I hope that this will be apparent from the examples that I will mention.

The role of both pre-formed and responsive defences is illustrated by the first of my examples, which is the colonization of the bark of beech, *Fagus* spp. by the beech scale insect, *Cryptococcus fagisuga* Lind. As a sucking insect, *C. fagisuga* removes materials in solution from individual cells of the cortex without ingesting structural components of the cells, which might be toxic or unpalatable to a biting insect such as a bark beetle. However, most sucking insects can feed on bark only if the outer corky layer is thin enough to allow insertion of their mouthparts into the cortex or phloem. For *C. fagisuga* on beech bark (Fig. 1), the penetrative depth of 1–2 mm is sufficient to allow feeding over most of the bark surface. Additionally, this insect's food source becomes enhanced by the stimulation of a gall-like growth of the cortical cells that surround the tip of its mouthparts (Hartig, 1878). In some cases, infestation is so heavy and continuous over the bark surface that the stem takes on a whitewashed appearance owing to the presence of the insect's white, woolly wax secretion (Fig. 2). In such cases, the growth of the tree is impaired, and the wood of the stem grows abnormally (Fig. 3) (Lonsdale, 1983). Heavy infestations also predispose the tree to a potentially lethal attack ("beech bark disease") by the fungus *Nectria coccinea* (Pers. ex. Fr.), which is otherwise usually incapable of causing much damage to beech trees (Lonsdale & Wainhouse, 1987).

The vulnerability of thin-barked trees like beech to attack by sucking insects may explain why other tree species normally develop a thick, rough bark as a pre-formed defence. Also, since a thick corky layer is a good thermal insulator and shock absorber, it helps to protect trees against injury from extremes of temperature (e.g. through sunscorch or forest fire) and from mechanical damage. Nevertheless, there



Fig. 1. Longitudinal section through bark of beech, *Fagus sylvatica*, showing penetration of mouthparts (stylets) of the beech scale insect, *Cryptococcus fagisuga*.



Fig. 2. A heavy infestation of a beech stem by the bark-sucking insect *Cryptococcus fagisuga*, Queen Elizabeth Forest, Hampshire. The white woolly wax secreted by the insects is conspicuous.

are advantages in having a thin bark. As, I have already mentioned, there is a place for economy in defence expenditure, and such an economy is achieved by minimizing the thickness of the outer corky bark. A thin corky layer also allows light to penetrate to the living cells beneath, so that the bark can contribute to photosynthesis. In the case of beech, chlorophyll can indeed be seen in the bark even of large old stems.

Of course things are not so simple that we can divide trees and shrubs simply into thick-barked and thin-barked species. Even in thick-barked species, at least the young twigs have a thin smooth bark. Like those of thin-barked species, they are at this stage enveloped by a simple primary periderm which expands to accommodate their increasing diameter. This smooth expansion ends sooner or later when the characteristic thick bark (rhytidome) starts to form through the development of



Fig. 3. Abnormal wood anatomy, with local reduction in annual ring width and parenchyma-like xylem cells, seen in a transverse section in the region of a colony of *Cryptococcus fagisuga*. The bark is at the right of the picture.

overlapping secondary periderms which arise in the outer phloem. In species where this "mature" bark forms only after many years, sucking insects have the opportunity to colonize the surface of stems of semi-mature trees. Even after this stage, there may still be localized sites in natural fissures where such insects can persist, and I shall mention an example of this later.

Although some tree species such as beech can retain a thin primary periderm throughout their lives, they also retain the ability to form a thickened bark ("pathological rhytidome") in response to injury. Thus, they can benefit from the advantages of reducing expenditure on cork production and from retaining photosynthetic capacity in the bark, while also being able to switch on a defensive response if necessary. A pathological rhytidome can often be seen in beech after several years' attack by *C. fagisuga* (Kunkel, 1968; Lonsdale, 1983; Ostrofsky & Blanchard, 1983). The resulting thickened, furrowed bark is more reminiscent of an elm or an ash than a beech.

When a beech stem forms a pathological rhytidome in response to prolonged feeding by *C. fagisuga*, the insect's feeding sites become restricted to the bases of fissures which form between the corky ridges of the rhytidome (Kunkel, 1968; Lonsdale, 1983). Even before this stage is reached, however, the initial feeding sites become unavailable due to the necrotic breakdown of the gall-like zones which previously served as enhanced food sources. It is this necrotic reaction which seems to trigger the development of "wound periderms" which eventually give rise to the pathological rhytidome.

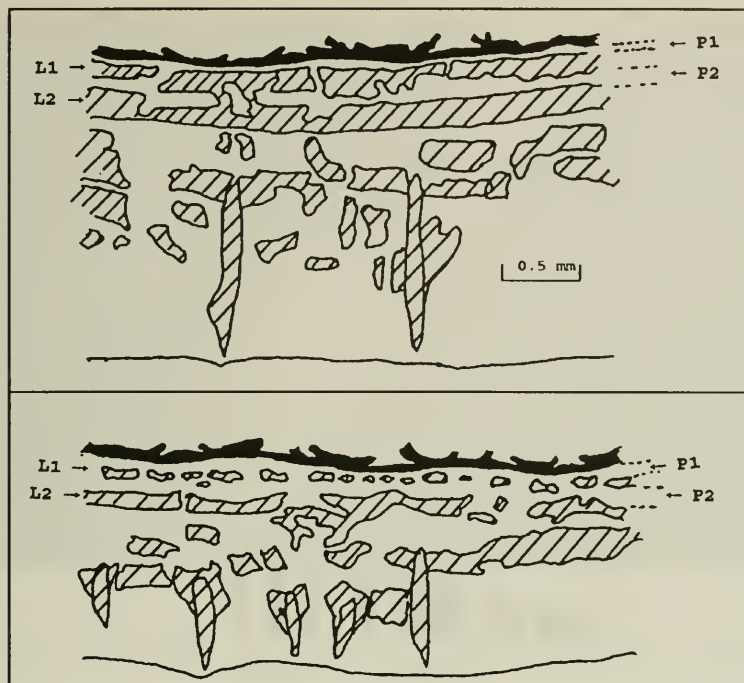


Fig. 4. Drawings of transverse sections of bark from beech trees whose resistance to attack by *C. fagisuga* was apparently high (above) or low (below); from Lonsdale (1983), ■ suberized tissue, ▨ lignified tissue, □ 'soft' tissue.

Although the primary periderm of beech is too thin to deter feeding by *C. fagisuga*, this does not mean that the bark as a whole lacks pre-formed defences. Within the living tissues beneath the periderm, there are heavily lignified cells (stone-cells) which provide a partial barrier to the penetration of the sucking mouthparts (Ehrlich, 1934). Lignin is a major structural constituent of wood, but its occurrence in other plant tissues is often associated with defence. Since colonization of beech by *C. fagisuga* can become very heavy despite the presence of lignified cells, the defensive role of lignin in beech did not at first attract much interest following the work of Ehrlich (1934). In the 1970s, David Wainhouse, one of my colleagues at Alice Holt Research Station, began to investigate genetic variation in resistance to *C. fagisuga*. He identified a number of beech clones of either high or low genetic resistance (Wainhouse & Howell, 1983), and I examined these to see whether they showed any obvious differences in bark anatomy.

I found that most of the relatively resistant trees identified by David Wainhouse had either a fairly unbroken sheet of stone-cells just beneath the corky periderm (Fig. 4), or a generally high content of such cells (Lonsdale, 1983). The resistant and susceptible clones could in most cases be distinguished anatomically by reference to an index, calculated from the relative thicknesses of the "soft" (parenchymatous) and "hard" layers of bark, and from the overall density of lignified cells (Fig. 5). Even

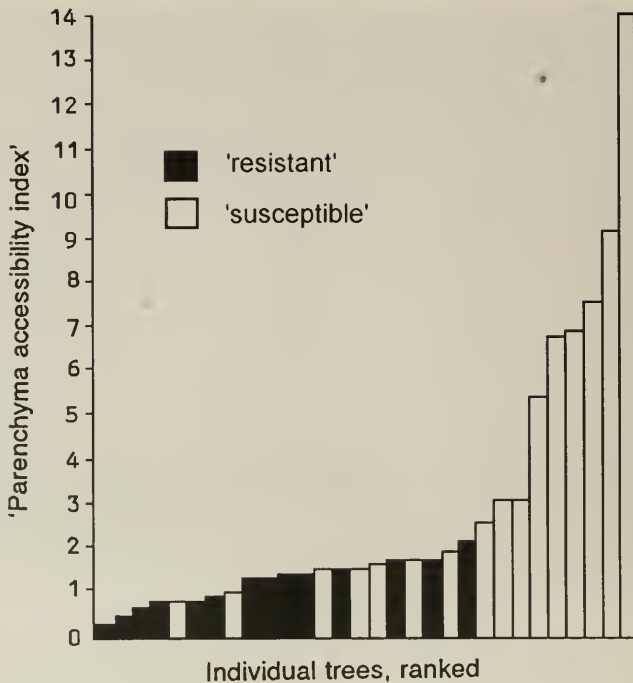


Fig. 5. Index values of the depth and accessibility of outer parenchyma (feeding zone) in beech trees with apparently high and low resistance to *C. fagisuga* attack; adapted from Lonsdale (1983).

$$\text{Bark accessibility index} = \frac{100 (P1 + P2)^2}{(\%L1 \times \%L2) (P1 + P2 + L1)}$$

where = $\begin{cases} P1, P2, L1 = \text{depths in } \mu\text{m of the corresponding layers in Fig. 4} \\ \%L1, \%L2 = \text{percentage lignin content of layers L1 and L2} \end{cases}$

relatively susceptible trees showed some ability to use lignin defensively, by laying down new lignin in the cell walls of tissues attacked by the insect.

Since, in a few cases, David Wainhouse found beech trees with an anatomically "susceptible" bark type which were quite resistant to attack by *C. fagisuga*, it was clear that other factors (probably chemical ones) were also contributing to resistance. The chemical explanation is borne out to some extent by another of his findings; that individual clonal lines of this parthenogenetic insect become adapted to their particular host trees (Wainhouse & Howell, 1983), a phenomenon known as 'host-tracking' (Edmunds & Alstad, 1978).

In North America, where *C. fagisuga* has the status of an introduced pest on the American beech, *Fagus grandifolia* (Ehrh.), this relative of the European beech also supports other bark-sucking insects. These include the beech blight aphid, *Prociphilus imbricator* Fitch, which can occur on main stems (Baker 1972), but



Fig. 6. The beech blight aphid, *Prociphilus imbricator*, Tunxis Forest Massachusetts.

often seems to prefer thin-barked twigs and even leaves (Fig. 6). Dense colonies of this woolly aphid are quite spectacular, since their members respond to disturbance by waving their abdomens, which bear long tufts of the insects' waxy secretion.

The feeding preferences of *P. imbricator* show that the age and thickness of bark, even on a thin-barked species like beech, affects food quality. If we look at tree species which normally develop a rhytidome, we tend to find bark-sucking insects largely confined to their twigs and small branches. Well known examples of such insects include the pine woolly aphid, *Pineus pini* (L.), and the large willow aphid, *Tuberolachnus salignus* (Gmelin) (Bevan, 1987). In the case of spruces, the periderm of the main stem tends to remain fairly thin until the tree has reached a considerable size, and thus allows feeding by the great black spruce bark aphid, *Cinara piceae* (Panz.).

Among those sucking insects that can occur even on thick-barked stems, though only in fissures, is the oak scale or "pox", *Kermes quercus* (L.). The oak scale, whose waxy capsules are visible as small shiny spheres, is associated with a dieback of oak in some parts of Britain. The prevalence of this disorder in the Forest of Wyre in Worcestershire has given it the name "Wyre pox". Another well known scale insect that is seen on thick-barked trees is the horse chestnut scale, *Pulvinaria regalis* Canard. Its hosts include several genera of broadleaved trees apart from *Aesculus*, these including *Acer*, and *Tilia*. The adult females of this insect are found on the main stem and large branches of the host, but this is merely their final resting place where they lay their eggs under a conspicuous waxy secretion. The immature stages feed in the crown of the tree, where there are soft shoots and thin-barked twigs and branches.

As I have mentioned, the solid constituents of bark tissues often include substances which deter feeding by biting insects, even on tree species that are susceptible to attack by bark-sucking insects. However, there is a major group of biting insects that are common in the bark of tree species belonging to many plant families. I refer to the bark beetles, which belong principally to the family Scolytidae. Many such beetles only attack environmentally stressed or moribund individuals, which are probably less able to manufacture anti-feeding materials as a defensive response. One of the most notorious bark beetles is the greater elm bark beetle, *Scolytus scolytus* (F.), which is one of the main vectors of the fungi which cause Dutch elm disease, *Ophiostoma* (Buism.) Nannf. and *O. novo-ulmi* Brasier. The transmission of these fungi occurs when beetles which have bred in the bark of moribund victims of the disease emerge and migrate to twig crotches of healthy trees, where they eat the young bark in their "maturation feeding" phase.

It is interesting that the lignin story crops up in relation to bark beetle attack, as well as in the case of the sucking insect, *C. fagisuga*, which I have already mentioned. Following my work on the stone-cells of beech bark, my colleague, David Wainhouse found that stone-cells in the bark of spruce, *Picea* spp., confer some resistance to the great spruce bark beetle, *Dendroctonus micans* Kug. This Eurasian beetle is not native to Britain, but was apparently imported here in the early 1970s on logs from the Continent (King & Fielding, 1989). It is rather unusual among bark beetles in that it can attack perfectly healthy trees. It does so by feeding communally, and also by virtue of its large size, both being attributes which help to overcome induced host resistance in the form of resin secretion. David Wainhouse has shown that the stone-cells in the bark of relatively resistant individuals of spruce confer partial protection by occurring in a layer which confines the larvae to a relatively narrow zone of soft tissue either above or below this layer. This confinement, perhaps together with the ingestion of some of the nutritionally poor stone-cells themselves, reduces the growth potential and survival of the larvae (Wainhouse *et al.*, 1990).

In many other relationships between trees and bark beetles, the size of larval galleries is probably determined by the thickness of the phloem layer that is available for feeding: either the total thickness of the soft zone of the phloem, or the thickness of a layer delimited by stone-cell barriers. This may account for the small size of bark beetle species which are able to feed in tree species with prominent stone-cell layers, such as *Ernoporus fagi* (F.) in beech.

These examples are just some of those for which research—led by an economic need—has revealed something of the fascination of the relations between bark-feeding insects and their hosts. I am sure that there must be many others for which field observations suggest the existence of equally interesting interactions.

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SHORT COMMUNICATION

***Dorcatoma dresdensis* Herbst (Coleoptera: Anobiidae) new to Gloucestershire.**—On 28.xi.1993, I collected a large piece of the bracket fungus *Ganoderma adspersum* (Schulz.) Donk. which had fallen from an ancient beech along the southern parish boundary of Rendcomb (SP 022089), E. Glos. The beech is one of a series along this boundary and which extend up the slope from Conigree Wood, an ancient woodland which has been much modified by Victorian plantings. The fungus was kept in a plastic box in a cool room and re-examined the following summer. Some 14 specimens of *Dorcatoma dresdensis* were found to have emerged, together with a few *Cis* and a parasitic wasp. This is the first time that this *Dorcatoma* has been reported from the county, although it is known from the adjoining counties of Oxfordshire (Cornbury Park in 1986, P. Hyman, pers. comm.) and Worcestershire (Whitehead, 1992), in both cases also on the Cotswold Limestone country. The Rendcomb locality is within 1 km of one of the county's best sites for saproxylic beetles, Rendcomb Park.

The species is otherwise only known from a thin scattering of ancient pasture-woodland sites in southern and eastern England. It was given red data book category 1 (endangered) status in Welch (1987) but this has since been revised to 'notable A' in Hyman & Parsons (1992), i.e. is believed to be confined in Britain to 30 or fewer 10 km squares. The reasons for the extent of the down-grading are not clear as I am only aware of records from about 10 other localities this century, with Windsor, Burnham Beeches and the New Forest being the only other records since 1980. RDB category 3 (Rare) seems to be more appropriate.—K. N. A. ALEXANDER, National Trust, 33 Sheep Street, Cirencester, Gloucestershire GL7 1QW.

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